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Microplankton biomass and diversity in the Vietnamese upwelling area during SW monsoon under normal conditions and after an ENSO event



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ABSTRACT

Investigating microplankton biomass and diversity under different climatological conditions is key to the understanding of cascading effects of climate change on nutrient cycles and biological productivity. Here we have used data collected during two contrasting summers along the coast of Viet Nam to show how climatological-driven changes can have a significant influence on the distribution of microplankton communities and their biomass via its impact on nutrient concentrations in the water column. The first summer in July 2003 followed a weak El-Nino Southern Oscillation (ENSO) event and was characterized by weak coastal upwelling, in the second summer during July 2004, upwelling was normal.

Very low silicate (SiO₄) concentrations and SiO₄:DIN ratios characterized the source water mass for upwelling in July 2004, and dynamic SiO₄ to dissolved inorganic nitrogen ratios (SiO₄:DIN) mainly below the Redfield-Brzezinski ratio and DIN to phosphate ratios (DIN:PO₄³⁻) below the Redfield ratio were a common feature off Viet Nam. Much higher particle concentrations and P_{Si}/PC ratios during normal upwelling revealed major changes in the microplankton community structure among summers. Small dinoflagellates (10–20 μm) prevailed ubiquitously during reduced upwelling. During normal upwelling, the diatom *Rhizosolenia* sp. dominated the cell-carbon biomass in the silicate poor upwelling waters. *Trichodesmium erythraeum* dominated in the Mekong-influenced and nutrient depleted offshore waters, where it co-occurred with *Rhizosolenia* sp. Both species were directly associated with the much higher primary production (PP) and N₂ fixation rates that were quantified in earlier studies, as well as with much higher diversities at these offshore sites. Along the coast, the correlation between *Rhizosolenia* sp. and PP rates was less clear and the factors regulating the biomass of *Rhizosolenia* sp. in the upwelling waters are discussed. The very low silicate concentrations in the source water mass for upwelling and the offshore deflection of the Mekong river plume likely triggered the observed ecological differences in the microplankton communities off Viet Nam in the normal upwelling season compared to the post ENSO conditions.

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1. Introduction

El Niño Southern Oscillation (ENSO) events can alter the phytoplankton community structure and biological productivity in the ocean (Behrenfeld et al., 2006; Chavez et al., 1999). ENSO events modulate the northern position of the Inter-Tropical Convergence Zone (ITCZ) and the intensity of both, South West Monsoon (SWM) and upwelling off Viet Nam (Dippner et al., 2013 and references therein). The impact of normal and reduced

upwelling conditions on the microplankton biomass and diversity has not been investigated off Viet Nam yet.

The SWM (also called summer monsoon) lasts from June to September and the stronger northeast (winter) monsoon appears from November to March. In 2004, the horizontal gradients in the sea level pressure were much steeper than in the post ENSO year 2003 according to Dippner et al. (2013). The consequences were much weaker southeasterly winds in July 2003 and a less pronounced northward propagation of the ITCZ. In the Vietnamese upwelling area, around 12°N, the wind speed was in the order of 2–3 m s⁻¹ during 2003, whereas during 2004, the speed was up to 6 m s⁻¹. The consequence was a much stronger upwelling in front

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of the Vietnamese coast during July 2004 compared to July 2003, which resulted in a completely different distribution of surface water masses (Dippner et al., 2013).

The upwelling area off Viet Nam is the most productive region in the South China Sea (Liu et al., 2002). During normal upwelling conditions in the SWM season in 2004 the rates of primary production and N_2 fixation off Viet Nam were much higher compared to the post ENSO SWM season in 2003, when upwelling was weak (Bombar et al., 2010; Voss et al., 2006). Changes in the nitrate, silicate, and phosphate concentrations, autotroph biomass, and phytoplankton community structure in the coastal waters are the primary causes for changes in primary production in other coastal upwelling areas (Blasco et al., 1981; Minas et al., 1986; Wilkerson and Dugdale, 2008 and references therein). The differences in the microplankton communities most likely underlying the large changes in the productivity off Viet Nam during normal, compared to reduced upwelling, have not been identified so far.

In this study, we analyzed the particle composition and the microplankton community structure including cell-carbon biomasses and diversities in the coastal waters off Viet Nam in July 2003 and July 2004. New nutrient data from the SWM season in 2004, spring inter-monsoon season in April 2004, and the late phase of the North East monsoon in March 2005 were compared to the published nutrient data set from July 2003 (Dippner et al., 2007). Further, we allocated the published primary production (Bombar et al., 2010) and N_2 fixation (Voss et al., 2006) rates to the respective water masses from which they were derived, and connected this information to the new microplankton cell-carbon data. This allowed us to construct a picture as to how nutrients prior to the growth season of phytoplankton influence the microplankton biomass, community structure, and productivity during normal upwelling conditions compared to reduced upwelling after an ENSO event off Viet Nam.

2. Material and methods

Four cruises took place in the center of the Vietnamese upwelling area (Fig. 1) with “MV Nghien Cuu Bien”: two cruises during SW monsoon, with one in July 2003 (VG-3, 18.–28. July 2003) after an ENSO event and the second in July 2004 (VG-7, 8–26. July 2004) under normal conditions, one during spring inter-monsoon in April–May 2004 (VG-4, 21.04.–02.05.2004), and one during the decaying phase of the NE monsoon in March 2005 (VG-8, 03.–13.03.2005). For VG-3 and VG-7, all parameters listed below were available, for VG-4 and VG-8, only nutrient data were available. Observations on a fixed station grid were carried out covering the area from 105°–111°E and 8°–14°N (Fig. 1).

At each station, CTD-observations, using a Sea-Bird Scientific® system, were made for temperature (T), salinity (S), depth (D), and fluorescence down to a maximum depth of 300 m. At oceanographic standard depths, water samples were taken, which were analyzed for nutrients (nitrate: NO_3^- , nitrite: NO_2^- , phosphate: PO_4^{3-} , and silicate: SiO_4), oxygen (O_2), particulate organic carbon (PC), particulate organic nitrogen (PN), particulate organic silicon (PSi), chlorophyll *a* (Chl. *a*), and phytoplankton cell counts. Immediately after sampling, water samples were filtered and measured by standard methods for nitrate, nitrite, and silicate after Grasshoff et al. (1983), and for phosphate after Murphy and Riley (1962). For chlorophyll *a* determination, 1–3 L of water were filtered through Whatman GF/F filters (nominal pore size of 0.7 μ m) and frozen (–20 °C) before further spectrophotometric processing after Jeffrey and Humphrey (1975). PSi was analyzed according to Bodungen et al. (1991). PC and PN measurements were made by a continuous-flow isotope mass spectrometer (Finnigan Delta S or Delta Plus) via a Conflow II open split interface.

Calibration for the PC and PN determination was done daily with an acetanilide standard. We conservatively estimate that the overall analytical precisions of our concentration measurements were better than $\pm 1.00 \mu$ mol for both nitrogen and carbon.

All microplankton samples were preserved with neutral Lugol's solution, and stored in the dark at 5 °C before analyses. Microplankton counts followed the Utermöhl method with modification (Larsen and Nguyen, 2004). Carbon biomass of microplankton was calculated using the cell volume with a minimum of 10 cells for each species/taxon (HELCOM, 2015) and computed by the software program Plankton-Sys 3.11 from Bioconsult A/S.

At selected stations, water samples were taken for incubation experiments to measure rates of primary production, N_2 fixation, and nitrate uptake, which have been published by Voss et al. (2006) and Bombar et al. (2010).

Taxonomic identification guides were from Hoang Quoc Truong (1962, 1963), Shiota (1966), Tomas (1997), and Larsen and Nguyen (2004). Heterotrophs and auto- and mixotroph assignments of dinoflagellates were based on HELCOM (2015) and Tomas (1997). Unidentified groups of thecate dinoflagellates were classed as mixotrophic, but may have included autotrophs and heterotrophs as well.

Water masses, in which the microplankton species/taxa were found, were identified using principal component analysis (PCA) of environmental variables. The temperature and salinity data and the biochemical variables of the discrete water samples for the PCA analysis were obtained from the CTD casts from the July 2003 data set from Dippner et al. (2007) and from the new July 2004 data set. The biochemical variables included concentrations of O_2 , SiO_4 , PO_4^{3-} , NO_3^- , NO_2^- , and Chl. *a*. Each water sample was allocated to a water mass according to the T/S based definition by Dippner and Loick-Wilde (2011). Water masses identified included the following: Mekong Gulf of Thailand Water (MKGW), Open Sea Water (OSW), Maximum Salinity Water (MSW), and the mixed water masses Water Mass 1 (WM1), Water Mass 2 (WM2), Water Mass 3 (WM3), and Water Mass 4 (WM4). The PCA was based on the Euclidean distance between the individual samples and was performed using PRIMER-6 Software (Primer-E Ltd., UK).

The data sets of the primary production, nitrate uptake, and N_2 fixation rates from Bombar et al. (2010) and Voss et al. (2006) were too small to be included in the PCA. Therefore, the allocation of the production rates to the different water masses was included in a separate Table 1.

The diversity of the microplankton species/taxa in the different water masses in July 2003 and July 2004 was estimated using the Margalef's index for species richness (*d*), Shannon-Wiener's diversity index (*H'*), and Pielou's evenness index (*J'*). All biodiversity indices used were based on the microplankton cell abundances.

The Margalef's index for species richness (*d*) is a measure of the number of species/taxa present for a given number of individuals (Clarke and Warwick, 2001):

$$d = \frac{S - 1}{\ln N} \quad (1)$$

where *S* is the number of species/taxa, and *N* is the total number of individuals in the sample.

Shannon-Wiener's *H'* is commonly used as a measure for species/taxa diversity in a community and accounts for abundance and evenness of the species/taxa present (Clarke and Warwick, 2001):

$$H' = - \sum_i p_i (\log_e p_i) \quad (2)$$

where *p_i* is the proportion of the total count arising from the *i*th species/taxa. Note that when comparing published indices it is

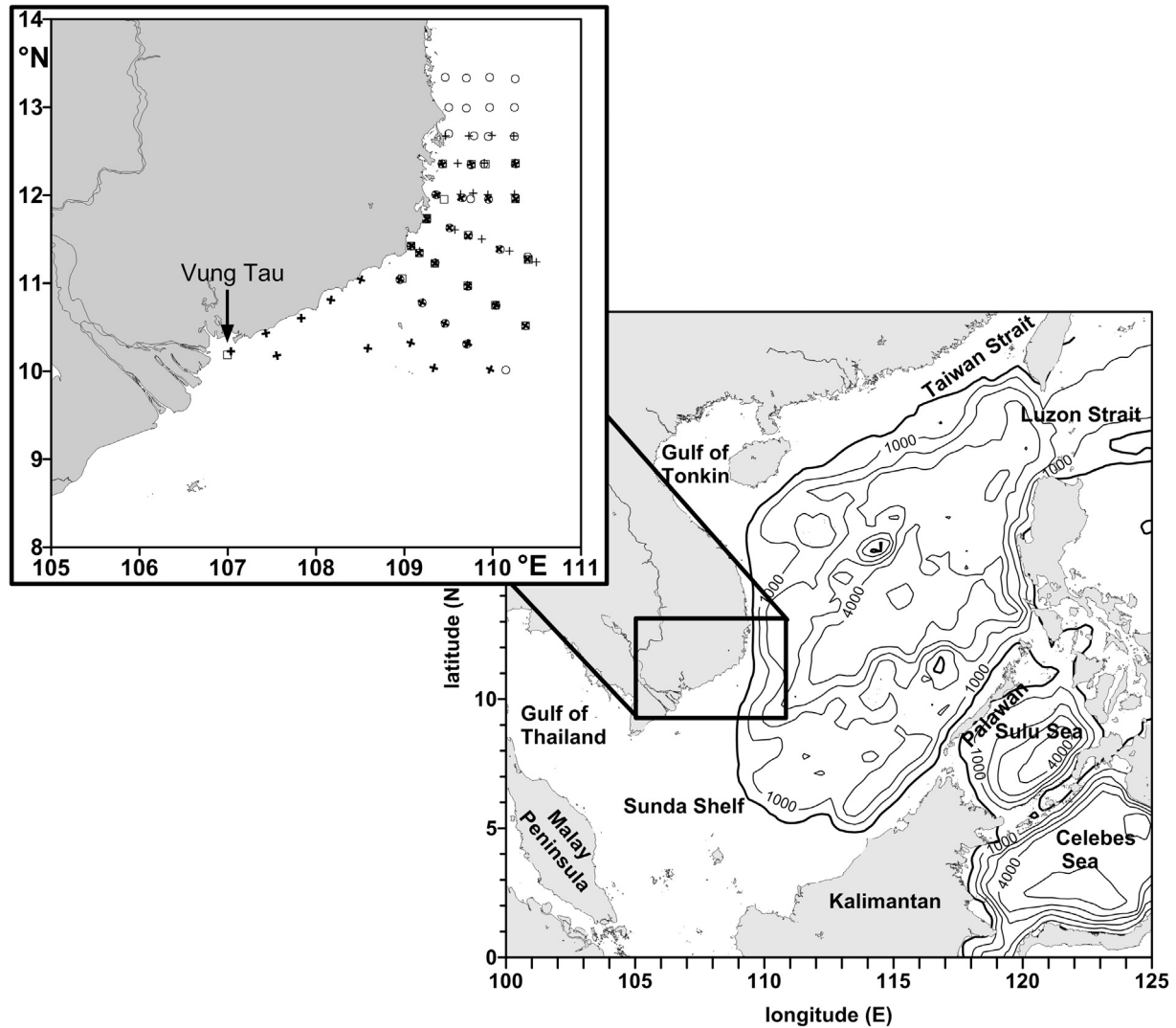


Fig. 1. Station map and topography map of the South China Sea modified from [Dippner and Loick-Wilde \(2011\)](#). The contour interval in the topography map is 1000 m. In addition, the shelf edge (200 m contour line) is marked by a bold line. The rectangle marks the area of investigation for the different cruises: VG3 (+) in July 2003, VG4 (○) in April 2004, VG7 (×) in July 2004, and VG8 (□) in March 2005. The position of the riverine endmember Station Vung Tau in the Mekong delta, where locally enhanced nutrient and particle concentrations were found, is indicated.

Table 1

Summary of gross primary production (PP), nitrate uptake (NP), and N_2 fixation (N Fix) rates (all in $nmol\ L^{-1}\ h^{-1}$) compiled from [Bombar et al. \(2010\)](#) and [Voss et al. \(2006\)](#), which were allocated to the respective water masses off Viet Nam in July 2003 and July 2004 as defined by [Dippner and Loick-Wilde \(2011\)](#). Given are the ranges for each variable followed by the number of observations. For some water masses, no production rates were determined (n.d.). Abbreviations of water masses: Mekong-Gulf of Thailand Water (MKGWTW), Open Sea Water (OSW), Maximum Salinity Water (MSW), and their mixed water masses WM4, WM3, and WM2 in 2003 and 2004, respectively. Note that NP rates in July 2003 and July 2004 corresponded to average specific nitrate uptake rates of $0.02 \pm 0.02\ d^{-1}$ ($n = 17$) and of $0.06 \pm 0.04\ d^{-1}$ ($n = 30$), respectively.

		PP	NP	N Fix
MKGWTW	2003	15.70–25.20 (3)	n.d.	0.07–0.20 (3)
	2004	144.70–194.70 (4)	n.d.	0.78–1.12 (4)
OSW	2003	2.90–34.60 (4)	0.10 (1)	0.01–0.04 (4)
	2004	1.80–63.70 (7)	n.d.	0.01–0.20 (8)
MSW	2003	0.70 (1)	0.38 (1)	0.01 (1)
	2004	n.d.	n.d.	n.d.
WM4	2003	25.40–137.30 (3)	0.90–6.10 (5)	0.01–0.05 (4)
	2004	21.80–347.60 (6)	0.77–9.50 (4)	0.02–0.07 (6)
WM3	2003	2.50–111.40 (12)	0.20–7.60 (4)	0.02–0.93 (13)
	2004	11.90–74.30 (13)	0.20–4.90 (3)	0.04–0.75 (16)
WM2	2003	0.00–59.10 (6)	0.10–2.50 (6)	0.00–0.05 (9)
	2004	30.00–395.20 (19)	0.50–20.00 (23)	0.02–0.20 (19)

important to check that the same logarithm base has been used in each case (Clarke and Warwick, 2001).

The Pielou's evenness index (J') for equitability quantifies how close in abundance each species/taxa is in an environment, given that there are at least two species/taxa present per location:

$$J' = \frac{H'}{H'_{\max}} \quad (3)$$

where H' is the number derived from the Shannon diversity index in Eq. (2), and H'_{\max} is the maximum diversity, which would be achieved if all species/taxa were equally abundant ($= \log_e S$, Clarke and Warwick, 2001).

We analyzed the dissimilarities of the species/taxon-specific cell-carbon biomasses in each water mass between July 2003 and July 2004 to identify the species/taxa that determined the differences in the microplankton communities between the two summers. The dissimilarities were analyzed by means of SIMPER (similarity percentages). The SIMPER analysis was based on the Bray-Curtis distance between the cell-carbon biomasses of the individual microplankton species/taxa averaged from the samples for each water mass and year.

All biodiversity indices and community dissimilarities were analyzed using PRIMER-6 Software (Primer-E Ltd., UK).

3. Results

Fig. 2A and B shows the monthly mean sea surface temperature in July 2003 and July 2004 respectively, obtained from AVHRR Pathfinder. In both SWM seasons, the averaged sea surface temperature across the SCS was in the order of 29–30 °C with local patches of more than 31 °C in the northwest corner of the Gulf of Thailand, northwest off the coast of Kalimantan, west of the Strait of Luzon, and in the Gulf of Tonkin (Fig. 2A and B). These patches were more pronounced during July 2003. Adjacent to the Vietnamese upwelling area, only very limited upwelling was detectable during 2003, whereas in July 2004 a strong upwelling signal was visible, along with an offshore transport of cold water into the central basin.

3.1. PCA of environmental data

We performed a factor analysis with the variables oxygen, nitrate, phosphate, silicate, nitrite, and chlorophyll *a* from all water masses from both SWM seasons (Table 2) to identify biochemical differences between them. The six variables used in the Principal Component Analysis (PCA) were reduced to the two dominant modes. The Eigenvalues of all Principal Components and the cumulative variance, as well as the loading components of the different variables in the two leading modes, are shown in the Supplementary Table 1. Generally, the first mode represented an axis of decreasing nitrate concentrations. The second mode represented an axis of increasing silicate concentrations. Together, they explained 92.5% of the variance. The Eigenvalues for the two modes were 2.24, and 0.43, respectively. The amount of explained variance in the leading modes were 77.4%, and 14.9%. In order to get a clear picture for any difference among the two years, the source water masses MSW, OSW, and MKGTW were displayed separately from their mixtures WM1 – WM4 in Fig. 3A–F.

According to the PCA, the deeper source water mass MSW had significantly higher nitrate concentrations compared to surface water masses OSW and MKGTW, while no differences in MSW nitrate concentrations were found between the two years (Fig. 3A and B, Table 2). In contrast to nitrate, clear inter-annual differences were found in the silicate concentrations in MSW, which were significantly higher during 2003, with concentrations

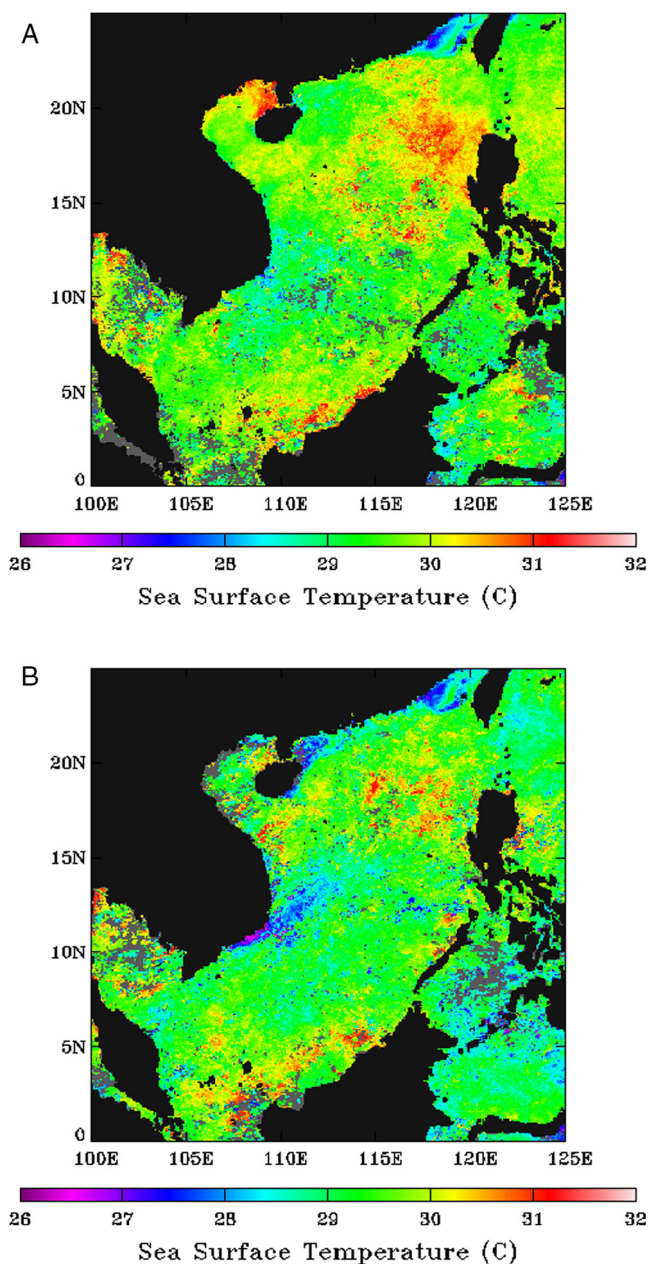


Fig. 2. Monthly mean sea surface temperature in (A) July 2003, and (B) July 2004 from AVHRR Pathfinder. Courtesy NASA/JPL/CalTech.

up to 19.6 μM compared to a maximum of 4.6 μM in 2004 (Fig. 3B, Table 2). The surface water masses MKGTW and OSW frequently contained measurable concentrations of nitrate and silicate, and frequently were depleted in both nutrients (Table 2) with little variability between the two years (Fig. 3A).

The arrangement of the water masses WM1, WM2, WM3, and WM4 along the Principal Components reflected the distribution of their respective source water masses. Nitrate and silicate concentrations were the main drivers for differences among the water masses, while silicate alone drove interannual differences within water masses, particularly those in the deep and subsurface (WM1, and WM2; Fig. 3C and D). Since WM1 and WM2 were mixtures of MSW with deeper water (WM1) and surface OSW (WM2), they arranged near MSW of the two-dimensional Principal Component Analysis ordination (Fig. 3C and D). WM3 and WM4 were surface and near surface water masses with impacts from MSW, OSW, and MKGTW resulting in the two-dimensional Principal Component

Table 2

Biochemical characterization of the water masses as defined by Dippner and Loick-Wilde (2011) including the Mekong-Gulf of Thailand Water (MKGTW), Open Sea Water (OSW), Maximum Salinity Water (MSW), and their mixed water masses (WM4, WM3, WM2, and WM1) in July 2003 (re-analyses of data from Dippner et al., 2007) and July 2004, respectively. Given are the ranges for each variable.

		O ₂ (μmol L ⁻¹)	NO ₃ ⁻ (μmol L ⁻¹)	PO ₄ ³⁻ (μmol L ⁻¹)	SiO ₄ (μmol L ⁻¹)	NO ₂ (μmol L ⁻¹)	Chl. <i>a</i> (μg L ⁻¹)
MKGTW	2003	141–147	0.0–0.1	0.0–0.1	0.0–4.1	0.0–0.0	0.2–0.3
	2004	75–172	0.0–1.1	0.0–0.2	0.6–3.8	0.0–0.8	0.3–3.3
OSW	2003	141–153	0.0–0.7	0.0–0.6	0.0–5.5	0.0–0.1	0.1–0.8
	2004	88–163	0.0–0.7	0.0–0.1	0.1–4.2	0.0–0.4	0.1–1.9
MSW	2003	84–144	7.0–14.0	0.5–1.0	1.3–19.6	0.0–0.1	0.0–0.6
	2004	72–172	9.6–17.3	0.7–1.2	1.7–4.6	0.0–0.2	0.0–0.5
WM4	2003	116–131	0.2–4.8	0.1–0.5	0.6–6.6	0.0–0.5	0.3–1.7
	2004	72–175	0.0–3.2	0.0–0.3	0.1–2.7	0.0–1.3	0.3–2.1
WM3	2003	134–144	0.0–1.7	0.0–0.3	0.9–5.1	0.0–0.1	0.1–1.2
	2004	66–172	0.0–0.1	0.0–0.0	0.6–3.7	0.0–0.0	0.1–6.5
WM2	2003	100–163	0.0–10.0	0.1–0.9	0.0–14.7	0.0–0.5	0.1–1.3
	2004	50–181	0.0–11.6	0.0–1.2	0.0–3.8	0.0–3.6	0.1–4.7
WM1	2003	84–103	10.1–20.0	0.0–1.4	9.8–24.7	0.0–0.1	0.0–0.3
	2004	66–166	13.6–19.7	1.0–1.6	2.1–6.3	0.0–0.2	0.0–0.1

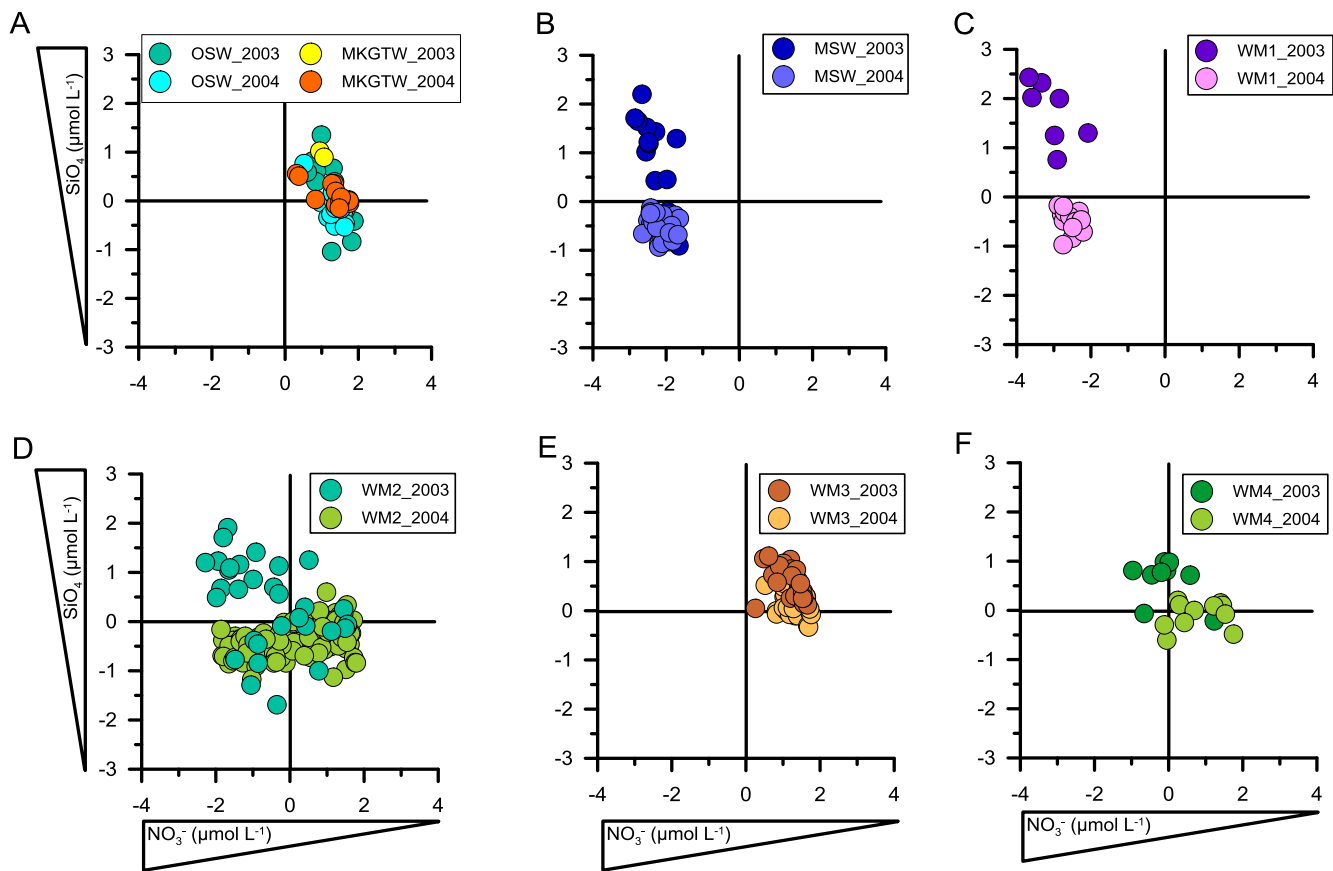


Fig. 3. Two-dimensional Principal Component Analysis ordination of the first two principal components (PC 1: x-axis; PC 2: y-axis) of the six environmental variables oxygen (O₂), nitrate (NO₃⁻), phosphate (PO₄³⁻), silicate (SiO₄), nitrite (NO₂), and chlorophyll *a* in the different water masses in July 2003 and July 2004 (see panel legends), respectively, for (A) the source water masses Mekong Gulf of Thailand Water (MKGTW) and Open Sea Water (OSW), (B) the source water mass for upwelling Maximum Salinity Water (MSW), and for the mixed water masses (C) Water Mass 1 (WM1), (D) Water Mass 2 (WM2), (E) Water Mass 3 (WM3), and (F) Water Mass 4 (WM4). The Eigenvectors of PC 1 and PC 2 were dominated by NO₃⁻ and SiO₄, respectively. Definition of water masses after Dippner and Loick-Wilde (2011).

Analysis ordination between those source water masses (Fig. 3E and F).

3.2. Dissolved nutrients and compounds of particulate organic matter

The PCA identified major differences in the nitrate and silicate concentrations among water masses, the latter showing additional changes in the water masses MSW, WM1, and WM2 between July

2003 and July 2004. The relationship between dissolved inorganic nitrogen (DIN: nitrate + nitrite) and SiO₄ therefore was further investigated by the inclusion of additional nutrient data from April 2004 and March 2005.

The DIN, PO₄³⁻, and SiO₄ concentrations showed a clear impact of low salinity waters from the Mekong river plume only in July 2004 at Station Vung Tau (DIN of 1.9 μM, SiO₄ of 3.8 μM, PO₄³⁻ of 0.2 μM, Supplemental Figs. 2–4), which is located in the Mekong

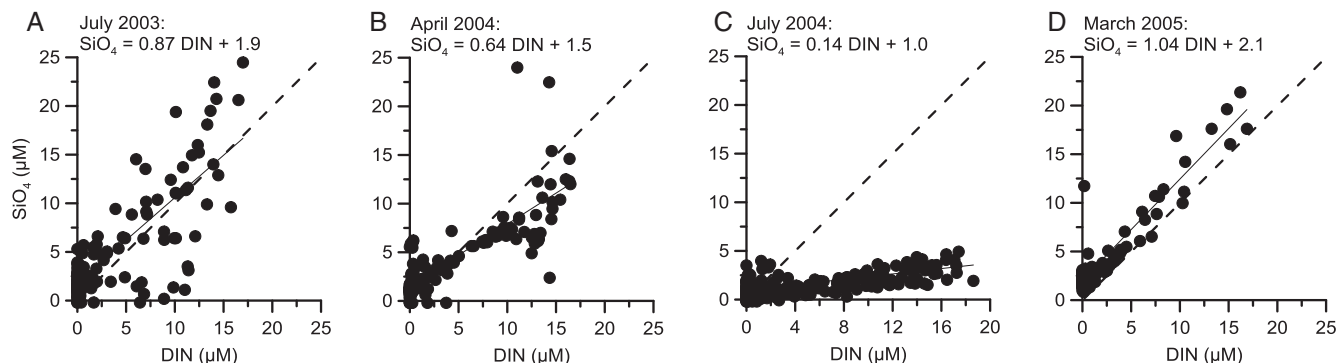


Fig. 4. The composite relationships between dissolved inorganic nitrogen (DIN: $\text{NO}_3^- + \text{NO}_2^-$ in μM) and dissolved silicate (SiO_4 in μM) in the upper 150 m off Viet Nam in July 2003 (A), April 2004 (B), July 2004 (C), and March 2005 (D). Average changes in SiO_4 :DIN relationships are shown by the slopes of the linear regressions during the different times of sampling. The Redfield-Brzezinski molar ratio of 1.04 (Brzezinski, 1985) is given as dotted line in each panel.

delta (Fig. 1). The absence of high nutrient concentrations from a riverine endmember made it evident that the water masses MSW and WM1 were the largest sources for all nutrients, including the seasonally changing SiO_4 concentrations.

The overall relationship between dissolved inorganic nitrogen (DIN: nitrate + nitrite) and SiO_4 concentration in the upper 150 m of the water column off Viet Nam between July 2003 and March 2005 is shown in Fig. 4A–D. Maximum SiO_4 concentrations in the upper 150 m of the water column clearly decreased from $24.7 \mu\text{M}$ in July 2003, to $15.6 \mu\text{M}$ in April 2004 (excluding two outliers in Fig. 4B), to $5.1 \mu\text{M}$ in July 2004, and then increased again to $21.6 \mu\text{M}$ in March 2005 without large changes in DIN and PO_4^{3-} concentrations (Supplemental Figs. 2–4). The change in SiO_4 concentrations was also reflected in the high variability of the SiO_4 :DIN ratios between July 2003 and March 2005 (0.14–1.04), with the minimum SiO_4 :DIN ratio of 0.14 in the data from July 2004 (Fig. 4A–D).

PSi concentrations more than doubled in 2004 (maximum PSi of $4.0 \mu\text{M}$, excluding Station Vung Tau in the Mekong delta) compared to 2003 (maximum PSi of $1.5 \mu\text{M}$) but PSi:PN ratios remained rather constant between July 2003 and 2004 (0.51 and 0.68, respectively, Fig. 5A and B). Furthermore, PSi concentrations showed significant linear correlations with PN and PC (Fig. 5C and D) concentrations (for all: $p < 0.001$) in both years. The PSi:PC ratios (Fig. 5C and D) were below the Redfield-Brzezinski ratio of 0.13 (Brzezinski, 1985) in 2003 (0.07) and almost at the Redfield-Brzezinski ratio in July 2004 (0.12). The PC:PN ratios (Fig. 5E and F) were above the Redfield ratio of 6.6 (Redfield et al., 1963) in 2003 (7.08) and below Redfield in 2004 (5.8).

3.3. Diversity

We analyzed the species richness, diversity, and evenness indices for each water mass and year based on the auto- and mixotroph microplankton species/taxa abundance (Fig. 6) as well as based on the total microplankton abundance including heterotrophs (not shown). A cluster analysis has also been tested, but the diversity in these tropical waters was too high to find any distinct pattern without significant reduction of stations (e.g. only looking at transects) and depth strata (e.g. only surface waters). We therefore proceeded with the water mass approach in order to include all samples.

The 2003 dataset included one cyanobacteria species (*Trichodesmium erythraeum*), 57 dinoflagellate taxa and three groups of thecate dinoflagellates of different size ranges (10–

$20 \mu\text{m}$, $20\text{--}50 \mu\text{m}$, and $>50 \mu\text{m}$), two taxa of dictyochophycean, 73 taxa of centric diatoms together with two groups of unidentified diatoms of the size range $20\text{--}50 \mu\text{m}$ and $>50 \mu\text{m}$, and 25 taxa of pennate diatoms together with two groups of unidentified pennates of the size ranges $20\text{--}50 \mu\text{m}$ and $>50 \mu\text{m}$.

In 2004 we found two cyanobacteria species (*T. erythraeum* and *T. thiebautii*), 98 dinoflagellate taxa and three groups of unidentified thecate dinoflagellates of different size ranges ($10\text{--}20 \mu\text{m}$, $20\text{--}50 \mu\text{m}$, and $>50 \mu\text{m}$), two taxa of dictyochophycean, 102 taxa of centric diatoms together with a group of unidentified diatoms of the size range $20\text{--}50 \mu\text{m}$, and 33 taxa of pennate diatoms together with two groups of unidentified pennates of the size ranges $20\text{--}50 \mu\text{m}$ and $>50 \mu\text{m}$.

Heterotrophic dinoflagellates (e.g. *Protoperidinium* spp., *Podolampas* spp., or *Oxytoxum* spp.) contributed 9% and 7% of all taxa and groups examined in 2003 and 2004, respectively.

In 2004 we found more auto- and mixotrophic species/taxa with contributions of less than 5% to the total abundance. This pattern was also reflected by higher Margalef's indices of species/taxa richness and Shannon diversity indices in most water masses (Fig. 6A and B). Highest species/taxa richness was found in the surface water masses MKGTW, OSW, WM3, and WM2 in 2004 (Fig. 6A). The highest evenness was found in the deeper water mass MSW and WM1, and the smallest differences in diversity and evenness among years was found in water mass WM4. A dramatic decline in all three indices was found in OSW and MKGTW with species richness decreasing in OSW by 58% and in MKGTW by 48% in 2003 compared to 2004. Shannon diversity decreased by 61% and 73% in MKGTW and OSW, respectively, and a switch from more equally abundant species/taxa towards dominance of single species/taxa were indicated by a decrease in equitability by 61% and 73% in MKGTW and OSW, respectively. Also in the water mass WM3, Shannon diversity and evenness declined considerably by 41% and 39%, respectively. Interestingly, *Rhizosolenia* sp. and *Trichodesmium erythraeum* cell-carbon biomasses in MKGTW, OSW, and WM3 were clearly higher in 2004 than in 2003 (Fig. 7).

3.4. Cell-specific carbon biomass and dissimilarity

In both years, the auto- and mixotroph carbon biomass values were highest in the water masses MKGTW (2.5 and $2.2 \mu\text{g C L}^{-1}$ in 2003 and 2004, respectively), WM3 (1.8 and $1.9 \mu\text{g C L}^{-1}$ in 2003 and 2004, respectively), and WM4 (1.6 and $1.7 \mu\text{g C L}^{-1}$ in 2003 and 2004, respectively) with little interannual differences (Fig. 7A). In contrast, auto- and mixotroph carbon biomass values decreased by 40% in OSW and increased by 100% in WM2 between 2003 and 2004 (Fig. 7A and B). In the deeper water masses MSW

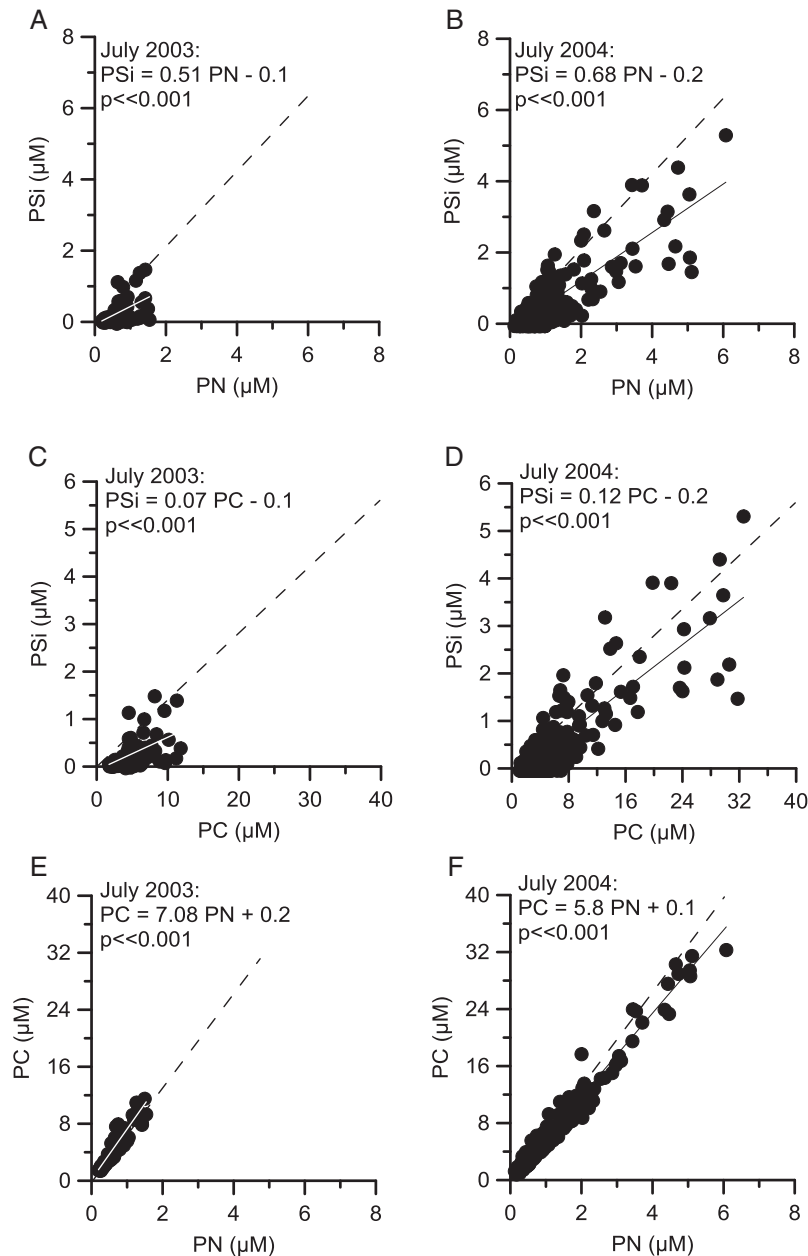


Fig. 5. The composite relationships between particulate nitrogen (PN) and particulate silicate (PSi) in μM in the upper 150 m in July 2003 (A) and July 2004 (B), between particulate carbon (PC) and PSi in μM in the upper 150 m in July 2003 (C) and July 2004 (D), and between PN and PC in μM in the upper 150 m in July 2003 (E) and July 2004 (F). Average changes in PSi:PN, PSi:PC, and PC:PN molar relationships are shown by the slopes of the linear regressions (black or white lines) during the different times of sampling. The respective Redfield (1934) and Redfield-Brzezinski (Brzezinski, 1985) molar ratios are given as dotted lines in each panel. Note that data from station Vung Tau was included in this data set.

and WM1, biomass was low in both years. Heterotrophic biomass ranged between 0.25 and $2.0 \mu\text{g cell-carbon L}^{-1}$ with maximum heterotrophic biomass values, namely of the dinoflagellate *Protopteridinium* spp., in the water masses WM3 ($2.0 \mu\text{g L}^{-1}$) and OSW ($1.2 \mu\text{g L}^{-1}$) in July 2003 (Fig. 8).

Despite the high percentage of auto- and mixotrophic taxa found in the study area (>90% of 300 total taxa examined), only 25 contributed >5% to the auto- and mixotroph cell-carbon biomass in both years (Fig. 9). Of those, only 3–8 taxa summed up to 43–84% of the auto- and mixotroph cell-carbon biomass in the respective water masses (Fig. 7B).

We analyzed the dissimilarities of the auto- and mixotrophic species/taxa cell-carbon biomasses in each water mass between July 2003 and July 2004 to identify the species/taxa that deter-

mined the differences in the microplankton communities between the two summers (Figs. 7 and 9). The dissimilarities among the communities in the same water masses were generally high but only 17 species/taxa explained >45% of the dissimilarities in all water masses (3–8 species/taxa per water mass) among years (Fig. 9). Small, thecate dinoflagellates (10–20 μm) explained most ubiquitously the dissimilarities in July 2003 but different diatoms also contributed to the dissimilarities among single water masses (Fig. 9). Only eight taxa driving the dissimilarities between the two summers were found in higher biomasses in the normal upwelling year 2004 (Fig. 9) including *Rhizosolenia* sp., *T. erythraeum*, *T. thiebautii*, *Cyclotella* sp., *Pleurosigma* spp., *Coscinodiscus* spp., *Cerataulina bergonii*, and *Guinardia striata* (Table 3). Only *Rhizosolenia* sp. occurred in all surface water masses in July 2004, with

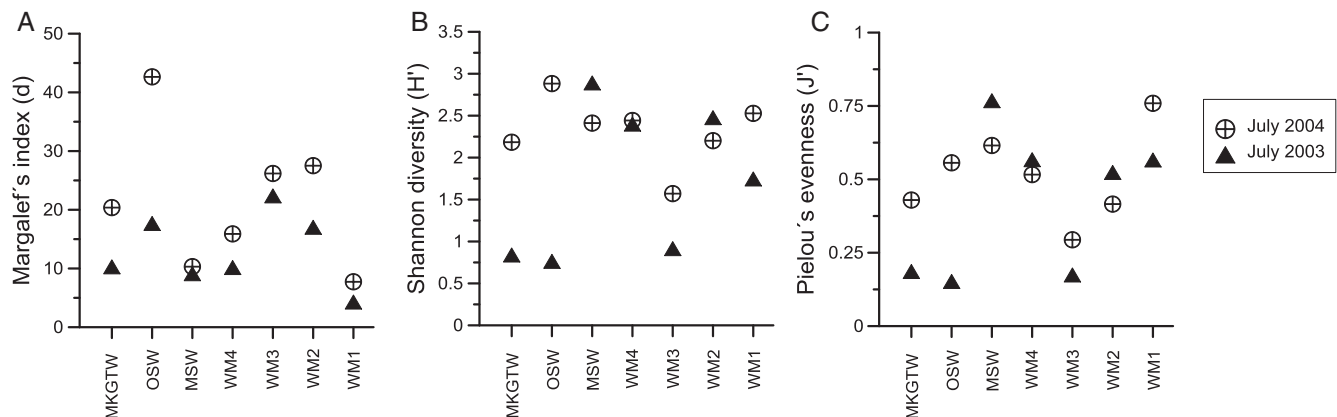


Fig. 6. Univariate indices for auto- and mixotrophic microplankton in the different water masses during the post ENSO July 2003 and during the normal upwelling season in July 2004 based on cell densities. (A) Margalef's species richness (d), (B) Shannon diversity (H'), and (C) Pielou's evenness (J'). Water mass abbreviations as in Fig. 3.

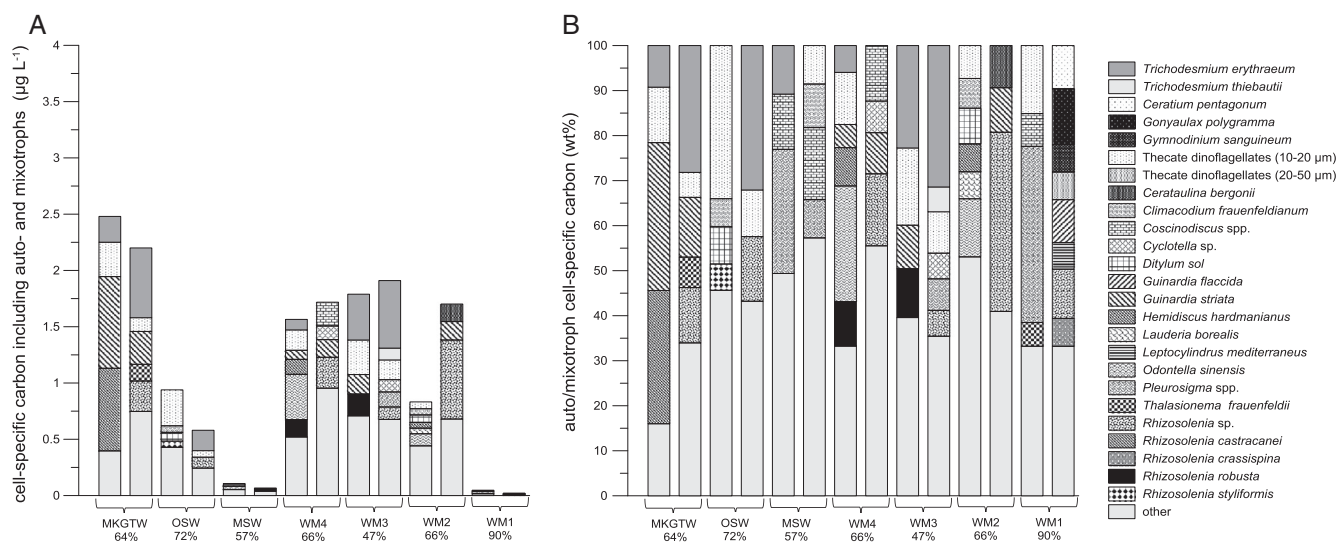


Fig. 7. Cell-carbon concentrations in $\mu\text{g C L}^{-1}$ (A) and weight% (wt%) carbon (B) of the 25 auto- and mixotrophic microplankton species/taxa that explained >5% of the total auto- and mixotroph biomass in the different water masses during July 2003 (left bars) and July 2004 (right bars). Individual taxa explaining <5% of total carbon were summed up as "other". Percent numbers below the water masses indicate community dissimilarities between July 2003 and 2004. Water mass abbreviations as in Fig. 3.

highest biomasses in the water masses WM2 and WM4 (Figs. 7 and 9). In the water masses MKGTW and OSW only *T. erythraeum* and *Rhizosolenia* sp. had higher biomasses in July 2004, with *T. erythraeum* always exceeding *Rhizosolenia* sp. biomasses (Fig. 9). The five other diatoms and *T. thiebautii* were distributed among the water masses WM2, WM3, or WM4 (Fig. 9).

In summary, small thecate dinoflagellates (10–20 μm) were the key taxon due to their ubiquitously higher biomasses in July 2003 (Fig. 9). *Rhizosolenia* sp. and *T. erythraeum* were the key species due to their ubiquitously higher biomasses in July 2004 (Fig. 9). *Rhizosolenia* sp. was the key species with higher biomasses in the water masses WM2 and WM4 where it also dominated the cell-carbon biomass in July 2004. *T. erythraeum* was the key species with higher biomasses in the water masses MKGTW, OSW, and WM3, where it also dominated the cell-carbon biomass in July 2004 although also *Rhizosolenia* sp. occurred in higher biomasses in these three water masses in July 2004 (Fig. 9).

4. Discussion

ENSO events are known to reduce the productivity, biomass, and diversity of phytoplankton in upwelling areas, e.g. off Chile (Escribano et al., 2004; Iriarte and González, 2004), Peru

(Codispoti et al., 1982), California (Chavez et al., 2002; Garate-Lizarraga and Beltrones, 1998; Wilkerson et al., 2002), or in equatorial upwelling areas of the Pacific (Dunne et al., 1999; Iriarte and Fryxell, 1995). The underlying causes include nutrient limitation and changes in nutrient ratios (e.g. decreases in $\text{SiO}_4:\text{DIN}$ and $\text{DIN}:\text{PO}_4^{3-}$ ratios) when oligotrophic, warm, oceanic waters overlay the cool, nutrient-rich waters or the origin of the water mass for upwelling is changed (Anabalón et al., 2016; Dugdale, 1972; Estrada and Blasco, 1979). Accompanied with these changes in surface waters are changes in the phytoplankton community structure, often a shift from a diatom to a dinoflagellate dominance in these areas (Anabalón et al., 2016; Estrada and Blasco, 1979). The observed changes in the microplankton diversity and biomass distribution off the coast of Viet Nam between 2003 and 2004 most likely were due to the modulating impact of the ENSO event on the nutrient distribution in the surface waters off Viet Nam and on a change in the $\text{SiO}_4:\text{DIN}$ ratio in the source water mass for upwelling MSW.

4.1. Changes in the water masses and nutrient distribution

In the Vietnamese upwelling area, limited upwelling occurred in July 2003, however the core of the upwelling water mass

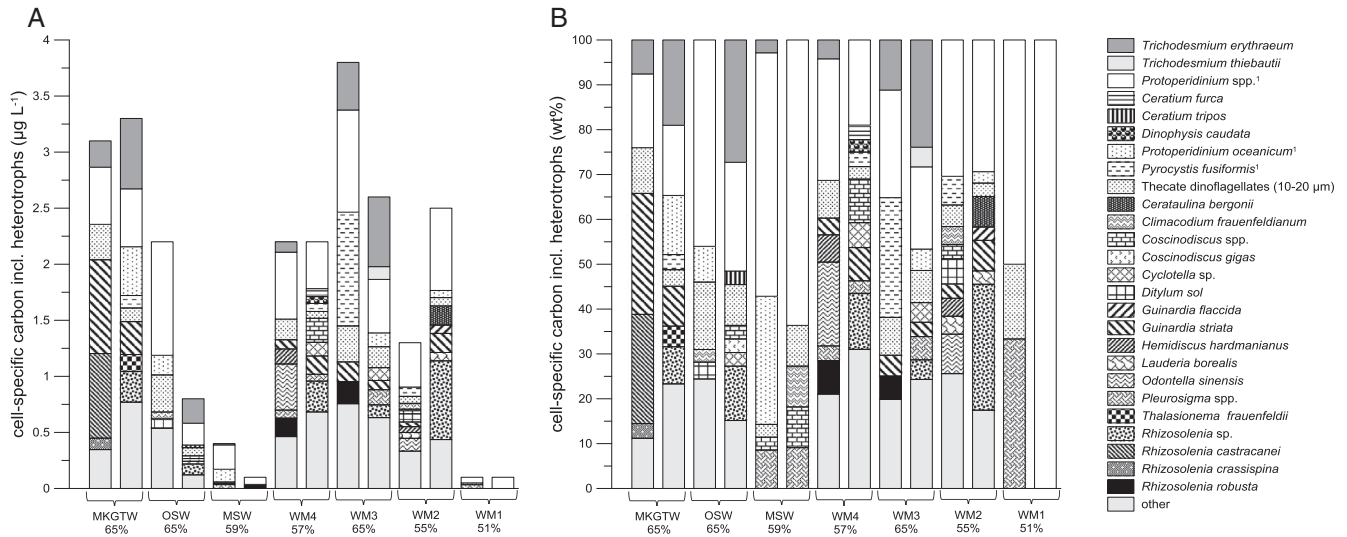


Fig. 8. Cell-carbon concentrations in $\mu\text{g C L}^{-1}$ (A) and weight% (wt%) carbon (B) of microplankton including heterotrophs¹ in water masses during July 2003 (left bars) and July 2004 (right bars). Individual taxa explaining <5% of total carbon were summed up as “other”. Percent numbers below the water masses indicate community dissimilarities between July 2003 and 2004. Water mass abbreviations as in Fig. 3.

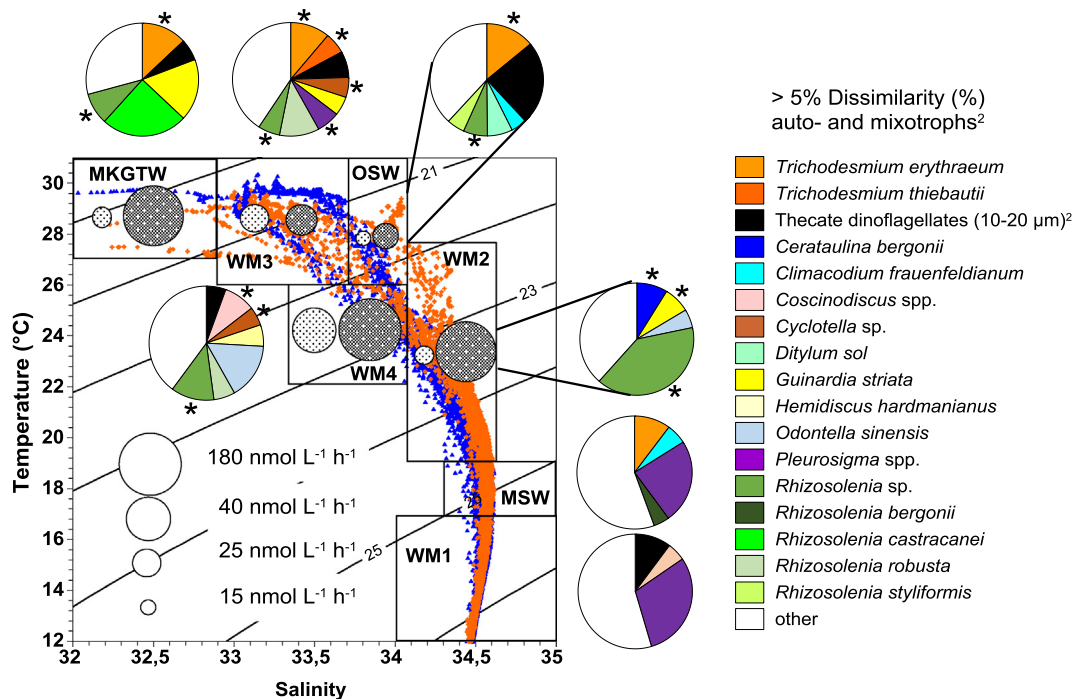


Fig. 9. Summary of the 17 auto- and mixotrophic phytoplankton species/taxa explaining >5% of the dissimilarities in the respective water masses between July 2003 and July 2004 (colored circles next to the water masses) and the average primary production (PP) rates (nmol $\text{C L}^{-1} \text{ h}^{-1}$) in the different water masses in July 2003 (left dotted circles) and July 2004 (right dotted circles) superimposed on the T/S profiles (2003: blue dots; 2004: red dots) of the respective water masses in a field of σ_t isolines. The asterisks on the right side of seven species in the dissimilarity plots indicate higher biomasses in July 2004. T/S-data from Dippner and Loick-Wilde (2011). Original PP rates for the allocation to the different water masses from Bombar et al. (2010). Water mass abbreviations as in Fig. 3.

WM2 did not reach the surface layers which were instead occupied by the coastal near water masses OSW and MKGTW (Dippner et al., 2007, 2013). The supply of nutrients in July 2003 was mainly regulated by dynamical upwelling due to the clock-wise rotation of the northward undercurrent that maintained high Chl. *a* concentrations in the subsurface water mass WM4 (Dippner et al., 2007).

In 2004, the stronger SW monsoon resulted in a strong wind-induced upwelling along the South Vietnamese coast (Fig. 1, Dippner et al., 2013). The upwelling water mass WM2 reached

the surface and the associated Ekman transport advected water masses WM2 and OSW offshore (Dippner et al., 2013, but see also Chen et al., 2012, 2013). The upwelling and offshore transport of WM2 and OSW resulted in a blocking of the coastal near northward transport of the Mekong influenced water masses MKGTW and WM3, which were deflected offshore (Dippner et al., 2013).

The nutrient distribution in the water masses off Viet Nam between July 2003 and March 2005 was characterized by DIN: PO_4^{3-} ratios below the Redfield ratio of 16 (Redfield et al., 1963)

Table 3

Some ecological characteristics of the microplankton species/taxa with higher cell-carbon biomasses in July 2004 compared to July 2003, and the water masses, where they occurred. The two key species in July 2004, *Rhizosolenia* sp. and *Trichodesmium erythraeum* and the water masses where they dominated the auto- and mixotroph cell-carbon biomass are highlighted in bold.

Species	Water masses	Ecology	Literature
<i>Rhizosolenia</i> sp.	WM2, WM4, MKGTW, OSW, WM3	Adapted to low DIN:PO ₄ ³⁻ ratios adapted to low SiO ₄ : DIN ratios large in size, causes high opal fluxes, positively or negatively buoyant adapted to upwelling waters	Villareal et al. (1999), Sommer (1998), Paul et al. (2008), Smith et al. (1996, 2001), Yoder et al. (1994), Villareal et al. (1993) and Lassiter et al. (2006)
<i>Trichodesmium erythraeum</i>	MKGTW, OSW, WM3	Diazotroph, large in size, buoyant, forms floating pelagic macro-environments	Capone et al. (1997), Paerl et al. (1989) and Hewson et al. (2009)
<i>T. thiebautii</i>	WM3	See <i>T. erythraeum</i>	See <i>T. erythraeum</i>
<i>Pleurosigma</i> spp.	WM3, WM4	May use internal silicate for growth	Tilman and Kilham (1976)
<i>Coscinodiscus</i> spp.	WM3	Light weighted biogenic silica valves	Sterrenburg et al. (2005)
	WM4	Adapted to upwelling areas high biomass in subsurface layers	Estrada and Blasco (1979), Mitchell-Innes and Walker (1991)
<i>Cerataulina bergonii</i>	WM2	Associated <i>Rhizosolenia</i> spp.	Passow and Peinert (1993)
<i>Guinardia striata</i>	WM2	Associated with <i>Rhizosolenia</i> spp.	Garrison et al. (1998) and Lassiter et al. (2006)

and by very variable SiO₄:DIN ratios (range of 0.14–1.04, Fig. 4) mainly below the Redfield-Brzezinski ratio of 1.04 (Brzezinski, 1985) due to changing silicate concentrations at constant DIN concentrations. A clear impact of low salinity waters from the Mekong River plume on DIN, PO₄³⁻, and SiO₄ distribution was not found for the upwelling area (Supplemental Figs. 2–4) and water mass MSW was the largest source of DIN, PO₄³⁻, and SiO₄ for the surface and subsurface waters in both SWM seasons (Table 2, Fig. 3B).

Interestingly, the SiO₄:DIN ratios in the upwelling water mass WM2 as well as in its source water mass MSW were clearly below the Redfield-Brzezinski ratio of 1.04 in July 2004 (0.2 ± 0.1 , $n = 55$). In contrast, the ratios were above the Redfield-Brzezinski ratio in July 2003 (1.2 ± 0.7 , $n = 59$). We can only speculate about what caused the formation of the different silicate concentrations in the water mass MSW. The origin of the coastal upwelling water may be on or off the shelf and the source depth may vary considerably, from depths of perhaps 200–400 m up to pycnocline depths depending on the intensity of upwelling, which may largely impact the silicate concentrations in surface waters (Dugdale, 1972; Mittelstaedt, 1991). Cyclonic and anti-cyclonic mesoscale eddies, which are thought to originate off Luzon (Xiu et al., 2010), are frequent features off central Viet Nam and elsewhere in the SCS (Wang et al., 2003). Interestingly, cold core eddies, which were characterized by silicate to nitrate ratios below the Redfield-Brzezinski ratio (range 0.14–0.89) at a depth of 75 m were situated off central Viet Nam in the summer and winter of the post ENSO year 1998 (Ning et al., 2004). In contrast, warm core eddies in the SCS in the same year were characterized by silicate to nitrate ratios clearly above the Redfield-Brzezinski ratio (Ning et al., 2004). The different SiO₄:DIN ratios in MSW between the post ENSO July 2003 and July 2004 thus could be related to varying impacts of cold and warm core eddies on the SiO₄ concentrations in the source water mass for upwelling, MSW, off Viet Nam. Further, a trail of sediments with low biogenic silica concentrations has been found between the Strait of Luzon and the upwelling area off southern central Viet Nam (Zhang et al., 2015). Clearly, the changing SiO₄ concentrations in the source water mass for upwelling, MSW, deserve further investigations.

In contrast to the much lower SiO₄ concentrations and SiO₄:DIN ratios in July 2004, the particle concentrations were much higher in July 2004 (Fig. 5). In July 2004, the higher P_{Si}:PC and P_N:PC ratios in nearly the Redfield and Redfield-Brzezinski ratios (Fig. 5) were indicative for large diatoms (Brzezinski, 1985). In July 2003, the P_{Si}:PN, P_{Si}:PC, and P_N:PC ratios corroborated apparent silicate uptake in a ratio that is typical for small diatoms (Brzezinski, 1985). These results suggest that small microplankton dominated the formation of the low particle concentrations in July

2003, while in July 2004 large diatoms dominated the formation of the much higher particle concentrations despite the very low ambient SiO₄ concentrations and SiO₄:DIN ratios. The high particle concentrations in July 2004 must have been the result of an approximate 66% higher primary production (PP) in July 2004 compared to July 2003 (Bombar et al., 2010).

4.2. Microplankton community in July 2003 vs. July 2004

Our dissimilarity analysis complemented the particle data concerning the major changes in the auto- and mixotrophic microplankton community structure between the post ENSO SWM season in July 2003 compared to the normal upwelling conditions in July 2004. Under post ENSO conditions in 2003, small (10–20 μm), presumably mixotrophic, thecate dinoflagellates were identified as the key taxon that reached ubiquitously high biomasses in surface water masses (Figs. 7 and 9). An increase in dinoflagellates has been observed in other upwelling areas at times of less turbulent water conditions (reviewed by Wilkerson and Dugdale, 2008). Such conditions were encountered e.g. in the upwelling region of the Baja California coast during weak upwelling (Mac Isaac, 1978; Walsh et al., 1974) or in upwelling areas with lower levels of NO₃, such as the Iberian upwelling system where picoplankton may play the most important role in NO₃ uptake (Joint et al., 2001). A similar mechanism likely also regulated the ubiquitously high biomasses of dinoflagellates off Viet Nam in the post ENSO season in July 2003 during reduced upwelling when less turbulent surface waters due to weaker wind prevailed with more depleted nutrient concentrations compared to July 2004 (Fig. 4). Further, the coastal near positions of the water masses MKGTW, OSW, and WM3 during reduced upwelling may have facilitated the occurrence of some diatoms in these water masses, which were maintained by the supply of nutrients from diffusion or the dynamical upwelling in subsurface waters.

In July 2004, we identified a split dominance in the cell-carbon concentrations from two ubiquitously occurring autotrophic key species with higher cell-carbon concentrations in July 2004. *Rhizosolenia* sp. was the key species in the coastal near upwelling water masses WM2 and WM4, and *T. erythraeum* was the key species in the warmer, and more nutrient depleted water masses MKGTW, OSW, and WM3 (Fig. 9) that were found much further offshore in July 2004 according to Dippner et al. (2013).

During both years, the cell-carbon biomass was very low in the two deepest water masses MSW and WM1, possibly due to light limitation of autotrophs.

A decrease in microplankton cell-carbon concentrations by up to 2 μg C L⁻¹ or in particulate organic carbon fluxes by >50% due

to ENSO events has been found in other tropical and subtropical areas like the Equatorial upwelling area in the Pacific (Iriarte and Fryxell, 1995), or the tropical upwelling areas off Peru and Chile (Escubano et al., 2004). Although the particle data indicated clearly higher phytoplankton concentrations during normal upwelling conditions, the cell-carbon biomasses, production rates, and diversities off Viet Nam did not increase consistently in the different water masses compared to the post ENSO conditions, pointing to unknown regulation mechanisms.

4.3. *Rhizosolenia* sp. in upwelling waters

Rhizosolenia sp. was the key species in the upwelling center in July 2004, where it dominated the auto- and mixotroph cell-carbon biomass in the water masses WM2 and WM4 (Figs. 8 and 9). Both water masses had in common that they were much cooler and that the water column probably was less stable compared to the offshore surface water masses MKGTW, OSW, and WM3 due to strong Ekman upwelling affecting WM2 and due to dynamical upwelling affecting WM4 in July 2004 (Dippner et al., 2007, 2013). Consequently, the supply of nutrients in the water masses WM2 and WM4 must have been more constant. This was supported by the maximum primary production rates that were found in both water masses in July 2004 (Table 1).

Only few diatom species (Table 3), namely the key species *Rhizosolenia* sp., were adapted to the very low $\text{SiO}_4:\text{DIN}$ ratios of 0.14 (Fig. 4) and to the low $\text{DIN}:\text{PO}_4^{3-}$ ratios of 13.7 (Supplementary Fig. 4) in the upwelling waters in July 2004. *Rhizosolenia* spp. have been found to be favored in growth by $\text{SiO}_4:\text{DIN}$ ratios <1 (Paul et al., 2008; Sommer, 1998) and may have profited from the very low $\text{SiO}_4:\text{DIN}$ ratios in the upwelling waters during normal upwelling conditions. A literature review (Table 3) on the ecological characteristics of the diatom species that had higher cell-carbon biomasses in July 2004 compared to July 2003 revealed that many of them share adaptations to low silicate concentrations and a preference for upwelling waters.

Among the seven different water masses off Viet Nam, only the upwelling water mass WM2, had clearly higher cell-carbon biomasses of auto- and mixotroph microplankton (1.6 vs. $0.8 \mu\text{g C L}^{-1}$ in 2004 vs. 2003, respectively) under normal conditions (Fig. 7). Light attenuation must have limited autotrophic growth in the nutrient rich waters from water mass WM2 in July 2003, when the coastal near, nutrient poor OSW covered WM2 during the post-ENSO conditions (Dippner et al., 2013). In 2004, WM2 was exposed to the surface (Dippner et al., 2013) and supported much higher cell-carbon biomasses e.g. of the diatom *Rhizosolenia* sp. (Figs. 7 and 9).

The auto- and mixotrophic cell-carbon biomasses in WM4 were almost congruent in July 2004 and July 2003 despite the high PP rates and *Rhizosolenia* sp. dominance in July 2004 (Fig. 7). In July 2003, high Chl. *a* concentrations were maintained in WM4 waters by dynamical upwelling in subsurface waters associated with the northward undercurrent that cannot be seen on satellite images (Dippner et al., 2007). The microplankton cell-carbon biomasses, namely of the key species *Rhizosolenia* sp., in relation to the primary production rates in the upwelling waters may shed light on the factors that prevented higher auto- and mixotroph microplankton cell-carbon biomasses in the water mass WM4 despite stronger upwelling in July 2004 (Fig. 10A).

Interestingly, the highest primary production (PP) rates in WM2 and WM4 waters occurred at minimum *Rhizosolenia* sp. cell-carbon biomasses in July 2004 (Fig. 10A). Bombar et al. (2010) noted that the maximum PP rates were realized in the actual upwelling center thus high PP rates at low *Rhizosolenia* sp. cell-carbon biomasses were not necessarily indicative for an early stage of a bloom (Mac Isaac et al., 1985). Nitrogen rather than silicate, phosphate,

or iron availability was suggested to be the most important control on primary productivity in the northern SCS (Chen et al., 2004; Wu et al., 2003). A specific trait of *Rhizosolenia* spp. is their ability to vertically migrate to avoid nitrogen limitation (Singler and Villareal, 2005). Further, different *Rhizosolenia* species can form diatom-diazotroph associations (DDAs) with N_2 -fixing *Richelia* sp. (Villareal, 1989). While DDAs including *Rhizosolenia*-*Richelia* symbioses are known to occur off southern-central Viet Nam (Bombar et al., 2011; Moisaner et al., 2008), *Rhizosolenia* mats, and internal nitrate storages in *Rhizosolenia* cells have not yet been identified. Potentially, these traits to avoid nitrogen limitation have contributed to the high cell-carbon biomasses of five different *Rhizosolenia* species in different water masses in both SWM seasons (Fig. 9). Nitrogen limitation thus may have been less severe for *Rhizosolenia* spp. growth compared to other diatoms and probably was not responsible for the decoupling between

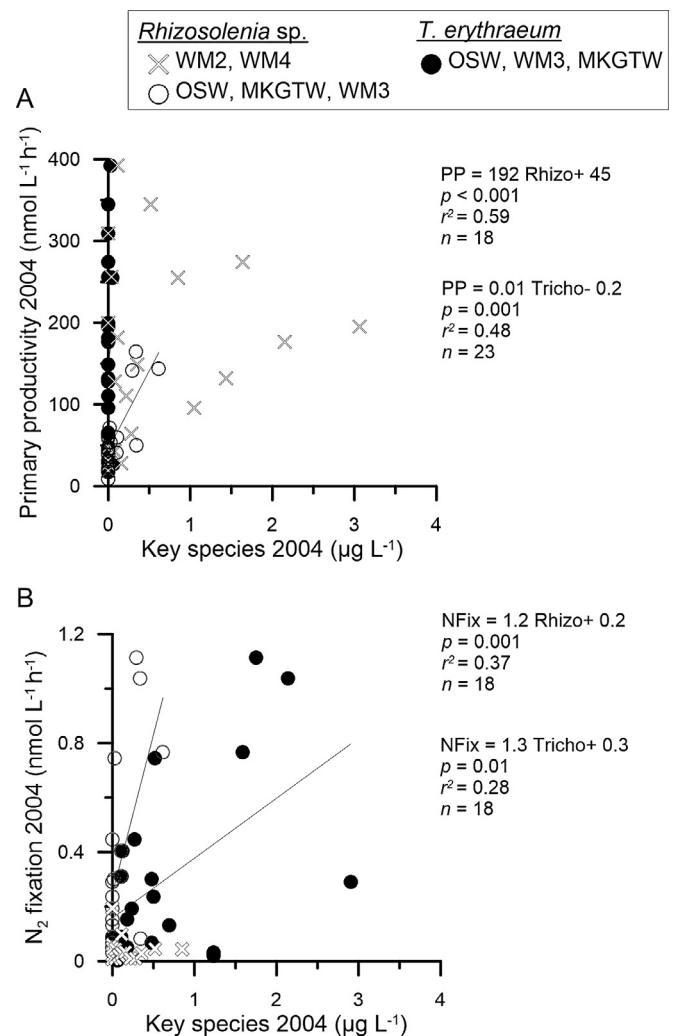


Fig. 10. The composite relationships between (A) primary production rates (PP) and (B) N_2 fixation rates (NFix) vs. cell-carbon biomasses of the key species *Rhizosolenia* sp. (Rhizo) and *Trichodesmium erythraeum* (Tricho) in the upwelling (WM2 and WM4) and offshore (MKGTW, OSW, and WM3) water masses, in which these species dominated or occurred in higher biomasses in July 2004 compared to July 2003. The linear regression lines indicate significant relationships between the variables at the offshore sites (see regression equations in the panels). No clear relationship was found for Rhizo and PP rates in the upwelling waters. Note that only negligible biomasses of *T. erythraeum* were found in the upwelling waters. Water mass abbreviations as in Fig. 3. Original PP and NFix rates for the allocation to the different water masses from Bombar et al. (2010) and Voss et al. (2006), respectively.

Rhizosolenia sp. cell-carbon biomass and primary production rates in the upwelling center (Fig. 10A).

Grazing of phytoplankton by herbivores cause at times a decoupling between autotroph cell-carbon biomass and primary production rates (Minas et al., 1986). We did not measure zooplankton grazing rates, but a potential impact of grazing on the autotrophic microplankton community was supported by the very low specific nitrate uptake rates of $0.06 \pm 0.04 \text{ d}^{-1}$ ($n = 30$, Bombar et al., 2010) in July 2004 despite strong upwelling. The nitrate uptake rates off Viet Nam in July 2004 were much lower than the high specific nitrate uptake rates of $0.2\text{--}0.8 \text{ d}^{-1}$ that were found in the non-grazing controlled and non-iron limited large eastern coastal upwelling areas off North and South America (Dugdale and Wilkerson, 1991). They were more similar to the very low specific nitrate uptake rates that were found in grazing controlled high nutrients low chlorophyll (HNLC) regions (Dugdale and Wilkerson, 1991). Grazing thus may have caused the observed decoupling between *Rhizosolenia* sp. cell-carbon biomasses and primary production rates in the upwelling waters.

4.4. *T. Erythraeum* and *Rhizosolenia* sp. in offshore waters

T. erythraeum was the key species in the offshore waters in July 2004, where it dominated the auto- and mixotroph cell-carbon biomass in the water masses MKGTW, OSW, and WM3 (Figs. 7 and 9). Besides *T. erythraeum*, also *Rhizosolenia* sp. contributed significantly to the microplankton dissimilarities in these water masses compared to July 2003 (Figs. 7 and 9). The N_2 -fixing and largely grazing-resistant cyanobacterium *T. erythraeum* prefers warm, stable, and DIN, but not iron or PO_4^{3-} depleted waters (Capone et al., 1997; Mulholland, 2007). The environmental conditions in the water masses OSW, MKGTW, and WM3 must have been more favorable for this species at their offshore position in July 2004 than at their coastal near position in July 2003.

Interestingly, the auto- and mixotroph microplankton cell-carbon biomasses in OSW waters were clearly lower and in MKGTW and WM3 waters, they were almost congruent in July 2004 compared to July 2003, despite the higher *T. erythraeum* and *Rhizosolenia* sp. cell-carbon biomasses in July 2004 (Fig. 7). In contrast to *T. erythraeum*, the diatom-specific cell-carbon biomasses were lower in the water masses MKGTW and OSW, and congruent in the water mass WM3 in July 2004 compared to July

2003 (Figs. 7 and 9). The offshore deflection of the water masses MKGTW, OSW, and WM3 (Dippner et al., 2013) possibly caused a limitation of growth of most diatom species (except for *Rhizosolenia* sp.) not adapted to the ambient low silicate and/or nitrate concentrations in July 2004. The water mass WM3 in July 2004 appeared to be a transition zone between the diatom dominated upwelling center and the *Trichodesmium* dominated offshore area as indicated by the co-occurrence of higher biomasses of *Trichodesmium* spp. and of the diatoms *Cyclotella* sp., *Pleurosigma* spp., and *Rhizosolenia* sp. (Fig. 9, Table 3). Further, only few organisms directly graze on *Trichodesmium* spp. (reviewed by Mulholland, 2007), which may have facilitated the observed dominance of *T. erythraeum* over *Rhizosolenia* sp. in the offshore waters in July 2004 (Figs. 7 and 9) despite the mentioned potential physiological adaptations of *Rhizosolenia* sp. to depleted DIN and very low SiO_4 concentrations.

We found strong indications that *T. erythraeum* and *Rhizosolenia* sp. regulated much of the higher primary production rates (Fig. 10A) in the offshore waters in July 2004. In a compilation of data from all three offshore water masses, primary production rates were significantly correlated with both, *T. erythraeum* and *Rhizosolenia* sp. cell-carbon biomasses in July 2004 (Fig. 10A). Interestingly, also the N_2 fixation rates correlated with the cell-carbon biomasses of both species in the water masses MKGTW, OSW, and WM3 in July 2004 (Fig. 10B). However, it remains unknown, if *Rhizosolenia* sp. received their nitrogen from diazotroph endosymbionts or in regenerated forms from *T. erythraeum*.

In summary, our findings extend the hypothesis by Voss et al. (2006) that the stability of the water column, and micronutrients and/or trace metals in the Mekong river plume may have been responsible for an enhanced productivity namely of *T. erythraeum* and *Rhizosolenia* sp. outside the upwelling center in July 2004. Further, they extend the suggestion by Bombar et al. (2010) and the offshore advection of regenerated nutrients and *Rhizosolenia* sp. cells from the upwelling center may have facilitated the high cell-carbon biomasses of both species at the offshore sites in July 2004.

4.5. Key species and microplankton diversity

Higher microplankton diversities frequently can be found during normal upwelling conditions compared to lower diversities

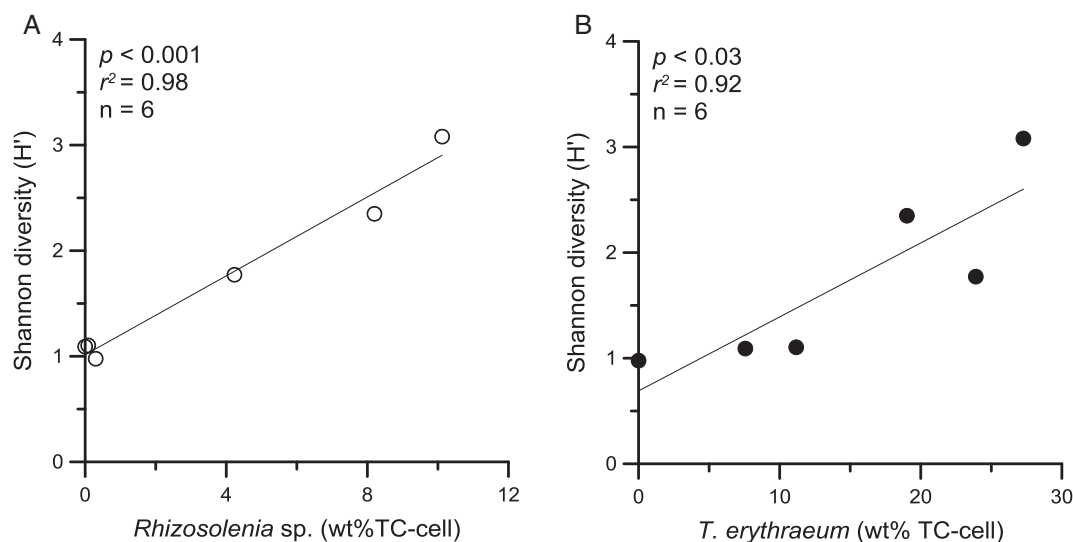


Fig. 11. *Rhizosolenia* sp. (A) and *Trichodesmium erythraeum* (B) weight% share of total microplankton cell carbon including heterotrophs (wt% TC-cell) vs. Shannon diversity (H') based on the cell abundances of the total microplankton species/taxa including heterotrophs in the warm surface water masses MKGTW, OSW, and WM3 in July 2003 and July 2004. Water mass abbreviations as in Fig. 3.

associated with ENSO events (Garate-Lizarraga and Beltrones, 1998). Off Viet Nam, the higher biomasses of *Rhizosolenia* sp. in the upwelling center were not accompanied by higher microplankton diversities in the water masses WM2 and WM4 (neither in the auto- and mixotrophic, nor in the total microplankton community including heterotrophs). Opal-rich *Rhizosolenia* spp. often cause peaks in the biogenic opal flux, e.g. in the Arabian Sea late in the upwelling season (Haake et al., 1993; Smith, 2001) or in the equatorial Pacific, where they form phytodetritus layers at the abyssal seafloor (Smith et al., 1996). Sediment records confirm intense accumulations of organic material in the Vietnamese upwelling area (Wetzel et al., 2011) although biogenic silica concentrations in sediment samples from the outer shelf (100–250 m depth) were low (Zhang et al., 2015). The fast sinking of large diatoms may prevent the development of a complex microbial food web as suggested for the diatom-dominated plankton community in the Amazon River plume (Loick-Wilde et al., 2015), thus preventing an increase in microplankton diversity.

Interestingly, at the offshore sites, the *Rhizosolenia* sp. weight% total cell-carbon biomass (including heterotrophs) was positively correlated with the diversity of the total microplankton community including heterotrophs (Fig. 11A). This was also the case for *T. erythraeum* with a less tight but still significant positive correlation (Fig. 11B). *Rhizosolenia* species may be positively or negatively buoyant and can form large mats in the tropical open ocean (Villareal et al., 1993; Yoder et al., 1994). A positive buoyancy may have facilitated the advection of *Rhizosolenia* sp. from the upwelling center into the offshore waters (Fig. 9). Also *Trichodesmium* spp. is positively buoyant and form large, floating macro-environments in the tropical, open ocean (Capone et al., 1997). Our results confirm observations that *Trichodesmium* spp. (Hewson et al., 2009; Paerl et al., 1989; Sheridan et al., 2002) and *Rhizosolenia* sp. (Pilskaln et al., 2005) form unique habitats in DIN depleted waters, which can contribute significantly to plankton heterogeneity in the open-ocean.

5. Conclusions

Here we only showed a snapshot in time, documenting the potential consequences of normal upwelling conditions compared to reduced upwelling during a post ENSO SWM season on the microplankton community structure off Viet Nam. Nevertheless, our water mass and community structure analyses in conjunction with prior studies imply that the factors light, stability of the water column, DIN:PO₄³⁻ ratios, SiO₄:DIN ratios, and grazing determined most of the microplankton biomass distribution in the different water masses. Adaptations to these factors allowed for the dominance of only few microplankton key species/taxa whose presence or absence largely determined the productivity and microplankton diversity in the different water masses off Viet Nam during normal and reduced upwelling conditions. Auto- and mixotrophic, small, thecate dinoflagellates occurred most ubiquitously in the less turbulent and nutrient depleted conditions during weak upwelling in July 2003. *Rhizosolenia* sp. and *T. erythraeum* were the key species that occurred most ubiquitously and that dominated the cell-carbon biomasses in- and outside the nutrient rich upwelling waters, respectively, under normal upwelling conditions in July 2004. *Rhizosolenia* sp. and *T. erythraeum* regulated much of the higher primary production rates described in earlier studies (Bombar et al., 2010), as well as of the microplankton diversity patterns in July 2004 compared to July 2003. Whether *Rhizosolenia* sp., like *T. erythraeum*, contributed to the higher N₂ fixation rates in July 2004 (Voss et al., 2006) remains unclear.

Very low SiO₄ concentrations observed in the source water mass for upwelling, MSW, and the offshore deflection of the

Mekong influenced water mass MKGTW likely triggered the observed ecological differences in the microplankton communities off Viet Nam during normal upwelling compared to the post ENSO conditions. A potential impact of normal conditions and ENSO events on the SiO₄ concentration of the source water mass for upwelling, MSW, deserves further investigation. Like the reduced upwelling in post ENSO years (Chao et al., 1996; Dippner et al., 2007; Zhang, 2000), ecological differences between a post ENSO SWM season and the following normal SWM season may be regular features off Viet Nam.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.poccean.2017.04.007>.

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